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1 **Scaling marine fish movement behaviour from individuals to populations.**

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7 **Running Head:** Scaling fish movement behaviour.
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Abstract

1. Understanding how, where and when animals move is a central problem in marine ecology and conservation. Key to improving our knowledge about what drives animal movement is the rising deployment of telemetry devices on a range of free-roaming species. An increasingly popular way of gaining meaningful inference from an animal's recorded movements is the application of hidden Markov models (HMMs), which allow for the identification of latent behavioural states in the movement paths of individuals. However, the use of HMMs to explore the population-level consequences of movement are often limited by model complexity and insufficient sample sizes.
2. Here, we introduce an alternative approach to current practices and provide evidence of how the inclusion of prior information in model structure can simplify the application of HMMs to multiple animal movement paths with two clear benefits: (1) consistent state allocation and (2) increases in effective sample size.
3. To demonstrate the utility of our approach we apply HMMs and adapted HMMs to over 100 multivariate movement paths consisting of conditionally dependent daily horizontal and vertical movements in two species of demersal fish: Atlantic cod (*Gadus morhua*; n=46) and European plaice (*Pleuronectes platessa*; n=61).
4. We identify latent states corresponding to two main underlying behaviours: resident and migrating. As our analysis considers a relatively large sample size and states are allocated consistently, we use collective model output to investigate state-dependent spatio-temporal trends at the individual- and population-level. Specifically, we show how both species shift their movement behaviours on a seasonal basis and demonstrate population space-use patterns that are consistent with previous individual-level studies.

5. Tagging studies are increasingly being used to inform stock assessment models, spatial management strategies and monitoring of marine fish populations. Our approach provides a promising way of adding value to tagging studies because inferences about movement behaviour can be gained from a larger proportion of datasets, making tagging studies more relevant to management and more cost effective.

Keywords: Atlantic cod, data storage tags, European plaice, hidden Markov modelling, movement behaviour, population-level patterns, priors.

1. Introduction

The spatial management of the marine world requires in-depth information about how animals move, when they move and where they move to. Key to increasing our understanding of species space use, movement patterns, and how individuals interact with the environment they inhabit, is the rising deployment of small and reliable data loggers and transmitters on free-roaming marine animals (Costa, Breed, & Robinson, 2012; Hussey et al., 2015; Hays et al., 2016). Capable of recording a range of movement metrics, including horizontal and vertical movement alongside basic environmental information such as water temperature, salinity and ambient daylight, these devices have revolutionized our understanding of fundamental ecology (Hussey et al., 2015), documented ocean-wide dispersal events (Block et al., 2011), highlighted areas that are essential for species survival (Raymond et al., 2015) and even allowed us to test the effectiveness of current conservation policies (Scott et al., 2012; Pittman et al., 2014).

One of the main motivations for animal-borne telemetry studies is that by understanding individual movement behaviour, we might infer the population-, species- and community-level consequences of movement (Block et al., 2011; Wakefield et al., 2011; Raymond et al., 2015; Hindell et al., 2016). This is especially true in marine systems, as individual observations provide our only insight into the otherwise unobservable. Achieving this scaling of inference from individual movement patterns to population dynamics requires two important components. The first is an adequate sample size (number of individuals) to address the ecological question of interest (Hebblewhite & Haydon, 2010) and second, a statistical means by which we gain meaningful

inference at the individual- and population-level from a finite sample of individuals (e.g. Langrock et al., 2012; McClintock, Russell, Matthiopoulos, & King, 2013; Jonsen, 2016).

The issue of sample size has been extensively discussed, especially when considering how movement studies can inform marine conservation and spatial management (Hebblewhite & Haydon, 2010; McGowan et al., 2017; Nguyen et al., 2017; Ogburn et al., 2017). Tags can be expensive (McGowan et al., 2017), are liable to occasional failure or loss and often result in individual pathways that are data-poor or have a low number of observations. As a result, meeting the minimum sample size of 20+ individuals when making simple statistical comparisons between populations is uncommon (Hebblewhite & Haydon, 2010), with even greater numbers needed when testing for the effects of age, sex and species identity (Lindberg & Walker, 2007). In the absence of a collaborative effort across multiple institutions (e.g. Block et al., 2011; Hindell et al., 2016), a significant increase in funding or a community wide shift to data sharing (e.g. via online data repositories like Movebank - Kranstauber et al., 2011); it would appear that the most viable route towards robust population-level inferences are approaches that make the most of the tagging data we already have.

Among the many methodological developments that utilize movement data to answer ecological questions, hidden Markov models and hidden semi-Markov models have taken centre stage (e.g. McKellar et al., 2015; DeRuiter et al., 2016; Michelot et al., 2016; Towner et al., 2016). Favoured because they match our intuitive understanding that movement is governed by switches in an animal's motivation (Patterson et al., 2017), HMMs provide a computationally efficient means of

objectively classifying movement into discrete states, with different statistical properties, indicating differences in underlying behaviour (Langrock et al., 2012).

HMMs have been fitted to multiple individual pathways simultaneously in both the frequentist (e.g. Langrock et al., 2012; McKellar et al., 2015) and Bayesian statistical paradigms (McClintock et al., 2013; Jonsen, 2016). However, these approaches are typically implemented by specialist statisticians and require the coupling of HMM and hierarchical structures, producing a hierarchical Hidden Markov model (HHMM). The alternative is the use of HMMs or other state-space approaches that fit on an individual by individual basis (e.g. Jonsen, Myers, & James, 2007; Michelot et al., 2017). This latter, more frequently used approach has its advantages, the most notable being an ease of use for statisticians and biologists alike. Fitting per individual also has its disadvantages. The first is that it requires individual movement paths that are suitably data-rich to achieve model convergence, imposing even stricter restrictions on sample size. The second is a distinct lack of any formal process by which state one in animal A is ensured consistency with state one in animal B. This lack of consistency means that estimated parameters can readily inform individual-level movement studies but will result in tricky interspecific and intraspecific comparisons, limiting a researcher's ability to ask *post-hoc* population-level questions of their data.

Our objective is to introduce an alternative framework that uses HMMs to overcome the described limitations of individually fitted HMMs whilst maintaining their heralded ease of use advantages. Our approach combines an N -state HMM and several hierarchical structures but bypasses the need to integrate over the random effects (as in HHMMs; Langrock et al., 2012) by using information

we gain from our data-rich pathways as *a priori* approximations of each states movement parameters. Doing so not only allows us to achieve coherent individual- and population-level state classification, but also ensures that we maximise our sample size by gaining meaningful inference from our data-poor and data-rich movement paths.

To illustrate our approach, we apply it to a real ecological problem – quantifying seasonal space use patterns in Atlantic cod (*Gadus morhua*) and European plaice (*Pleuronectes platessa*) in the North Sea and English Channel. Both Atlantic cod and European plaice have significant commercial and conservation value and as a result have been the subject of several long-term tagging programs (e.g. Righton, Metcalfe, & Connolly, 2001; Hunter, Metcalfe, Arnold, & Reynolds, 2004; Hunter, Metcalfe, O’Brien, Arnold, & Reynolds, 2004; Hobson, Righton, Metcalfe, & Hays, 2007, 2009). Drawing on this, the rest of this paper considers a case study of 107 individual bivariate movement paths, many of which (n=73) have limited observations and/or lack clear biological signals. Our findings demonstrate clear spatio-temporal patterns in the movement behaviour of either species that are consistent with individual-level studies (Hunter, Metcalfe, Arnold, et al., 2004; Hunter, Metcalfe, O’Brien, et al., 2004; Hobson et al., 2007, 2009; Neat et al., 2014). Furthermore, by analyzing a relatively large dataset, we provide a unique insight into how differing sub-stocks of cod and plaice shift their behaviour on a seasonal basis, with clear consequences for fisheries management and conservation.

2. Materials & Methods

2.1. Case study data

Movement paths were taken directly from the deployment of data storage tags (DSTs) on free-roaming fish in the North Sea or English Channel. The dataset includes 107 individuals from two species of European demersal fish: Atlantic cod (n=46) and European plaice (n=61). All fish were tagged and released between December 1996 and June 2011. Fish were broadly separated into substocks based on release location (see Figure 1) and displayed considerable variation in movement path duration (Table S1).

Each DST was programmed to record depth (m) at 10-minute intervals for the duration of deployment. The first two weeks and the last day of every time series were excluded to remove any erroneous or irregular measurements associated with release and recapture events as per Hobson et al., (2007). For details of tag type, fish catchment, tag implantation and measurement accuracy see Righton et al. (2010; *Gadus morhua*) or Hunter, Metcalfe, Arnold, et al. (2004; *Pleuronectes platessa*).

Each movement path is a bivariate time series of horizontal and vertical movement per day. Net vertical movement (m day^{-1}) of each fish was taken directly from the raw DST data by calculating the absolute difference between corresponding 10-minute depth measurements and summing the values for each day at liberty. Horizontal movement (m day^{-1}), in comparison, was inferred indirectly from the depth data in a two-step approach. First, daily geolocation estimates were produced via a Fokker-Planck-based method that combines Metcalfe & Arnold's (1997) tidal location method and a Bayesian state-space model (see Pedersen, Righton, Thygesen, Andersen, & Madsen 2008 for model details). The straight-line distance between daily geographic estimates

(commonly referred to as ‘step-length’) was then calculated using the Great Circle equation. Both vertical (v) and horizontal (h) movement metrics were log (natural log) transformed prior to model implementation. Only time series that were longer than 40+ days and had complete depth recordings were used in this study. For descriptions of horizontal and vertical movement in Atlantic cod and European plaice see Hunter, Metcalfe, Arnold, et al. (2004), Hunter, Metcalfe, O’Brien, et al. (2004) and Hobson et al. (2007; 2009).

2.2. The model

Previous individual-level studies demonstrate that Atlantic cod and European plaice display periods of high activity while in the water column punctuated by periods of relatively low activity while on the seabed (Metcalfe, Hunter, & Buckley, 2006; Righton et al., 2010). Thus, we consider a discrete 2-state HMM. We label state one as ‘resident’ (R), representing periods of time with low movement rates. We label state two as ‘migrating’ (M), representing a much more active phase where movement rates in the horizontal and vertical dimension are greatly increased. As in all attempts to infer behaviour from movement observations, state labels must be interpreted with care as they provide simplified proxies of unobserved behavioural modes, not direct equivalents (Patterson et al., 2017).

For a movement path of length T , it is assumed that an underlying, non-observed state sequence S_1, \dots, S_T , taking values in $\{R, M\}$ describes the persistence within and stochastic switching between states. The time varying evolution of this state process takes the form of a (first-order) Markov chain, with transition probability matrix Γ

218

219

$$\Gamma = \begin{pmatrix} \gamma_{R \rightarrow R} & \gamma_{R \rightarrow M} \\ \gamma_{M \rightarrow R} & \gamma_{M \rightarrow M} \end{pmatrix} \quad [1]$$

220 and

221

$$\gamma_{j \rightarrow k} = \Pr(S_{t+1} = k \mid S_t = j) \quad [2]$$

222

223 for any j, k in $\{R, M\}$. Given a state j at time t the observation x_t is assumed to be drawn from a
224 multivariate normal distribution (MVN):

225

$$x_t \sim MVN(\mu_j, \Sigma_j) \quad [3]$$

226 with

227

$$\mu_j = \begin{pmatrix} \mu_{jH} \\ \mu_{jV} \end{pmatrix} \quad [4]$$

228 and

229

$$\Sigma_j = \begin{pmatrix} \sigma_{jH}^2 & \rho_j \sigma_{jH} \sigma_{jV} \\ \rho_j \sigma_{jH} \sigma_{jV} & \sigma_{jV}^2 \end{pmatrix} \quad [5]$$

230

231 and H and V represent movements made in the horizontal and vertical dimension, respectively.

232 Thus, the complete-data likelihood given a state sequence S_1, \dots, S_T is

233

234

$$\omega_{S_1} \phi_{S_1}(x_1) \gamma_{S_1 \rightarrow S_2} \phi_{S_2}(x_2) \dots \gamma_{S_{T-1} \rightarrow S_T} \phi_{S_T}(x_T) \quad [6]$$

235

236 where the row vector ω is the Markov chain initial state probability (which we assume to be

237 uniform at $t=1$) and ϕ_j refers to the multivariate normal density stated in equation 3. We allow

238 distinct parameters for each fish, indexed by $i = 1, \dots, 107$, and write these as Γ^i , μ_j^i and Σ_j^i .

239

240 In practice, standard HMM algorithms allow us to calculate the actual likelihood, when the states
241 are unobserved, very efficiently by integrating over all possible state sequences using the forward
242 algorithm (Zucchini, MacDonald, & Langrock, 2016). Framing the model in this way enables us
243 to conduct parameter estimation using a Bayesian approach, by numerically maximising the
244 posterior density. The classification probability of each state at t is then determined using the
245 backward smoothing algorithm (Zucchini et al., 2016). More details for how the efficient HMM
246 machinery can be used to conduct statistical inference are given in Zucchini et al. (2016), for the
247 particular case of animal movement modelling see Patterson et al. (2017). For our case study, we
248 used the R optimisation routine *optim* to numerically maximize the log posterior density. State
249 allocation is carried out by selecting the most likely state at each time point separately.

250

251 Periods of relative inactivity (low h and v movement rates) can persist for 3-5 months in either
252 species (Metcalf et al., 2006; Righton et al., 2010). To accommodate this persistence within state,
253 we have imposed a prior penalty term on the transition probabilities, such that

254

$$255 \qquad \qquad \qquad \gamma_{11} \sim \text{beta}(\alpha, \beta) \qquad \qquad \qquad [7]$$

256 and

$$257 \qquad \qquad \qquad \gamma_{22} \sim \text{beta}(\alpha, \beta) \qquad \qquad \qquad [8]$$

258

259 where $\alpha = 99$ and $\beta = 1$. This prior, termed here after as the transition probability prior, is designed
260 to ensure that states R and M correspond to strong seasonal shifts in movement behaviour and not
261 day-to-day fluctuations.

2.3. Classifying fish movements

We apply the model described in section 2.2. to all 107 individual movement paths, such that each fish gets its own parameter set. Each parameter set consists of 12 estimated parameters, two transition probabilities and 2 sets of 5 parameters describing the mean (μ_j) and covariance (Σ_j) of each state. A total number of 24,624 days (Atlantic cod = 9290 days; European plaice = 15,334 days) were considered. As expected, the resulting state sequences are predominately made up of two clearly defined behavioural modes – one more active and one less active (see Figure S1 and S2 for example output). However, the parameters describing the numerical structure of these modes showed great variation among fish, with no clear consistency. Moreover, a handful of movement paths failed to achieve model convergence, as an upper threshold of observations is needed for robust parameter estimation (Patterson, Basson, Bravington, & Gunn, 2009).

To avoid the wasteful removal of valuable data or a tedious *post-hoc* description of the individual variation that exists in the HMMs output, we adopted an alternative approach. Based on the selection criteria outlined in Figure S3, we select model output from 34 fish (Atlantic cod, n=11; European plaice, n=23) spread evenly across the five sub-stocks (Table S2). We then calculate summary statistics (means m and variances δ) that describe the numerical structure of the two states (Figure S4). These summary statistics are used to construct Gaussian distributions (Figure 2), $N(m, \delta)$ where m and δ are dimension (h or v) d , state j and species specific given the selected sample. These informative distributions (4 per species), termed here after as priors on the model's

movement parameters, are then introduced directly into the HMMs likelihood function, such that equation 6 is multiplied by

$$\prod_j \prod_d \phi(\mu_{jd} | m_{jd}, \delta_{jd}) \quad [9]$$

where $\phi(\cdot | m, \delta)$ is the Gaussian density with mean m and variance δ . Thus, our informative priors act to constrain the mean parameters of each state during the classification process.

This adapted approach is applied to the classification of the remaining 73 individual pathways (Atlantic cod, $n=35$; European plaice, $n=38$), outputting state sequences that comprise comparable states across all fish. This enables *post-hoc* comparisons to be made at the individual- and population-level with relative ease. For an example of how prior inclusion influences the classification process see Figure S5. Furthermore, demonstrations of how comparable states are across multiple fish (Figure S6) and differences between model fit for one of the data-poor movement paths are provided (Figure S7).

All HMMs were coded and implemented in R (R Core Team, 2016; see Supplementary Information document 2 for example code). All plots were generated using the *ggplot2* (Wickham, 2009) and *ggmap* (Kahle & Wickham, 2013) packages in R (R Core Team, 2016). Bathymetric data was sampled from the General Bathymetric Chart of the Oceans online repository (GEBCO, www.gebco.net), which is a global topographic dataset with a one-minute spatial (1') spatial resolution.

2.4. Prior sensitivity analysis

When imposing prior distributions in statistical models it is always important to test what influence those priors have on the models' predictions, in our case the model's estimated state sequences. To test the sensitivity of our model to changes in the transition probability prior we varied the α and β values that characterise the priors' beta distribution and re-ran the HMM for all 34 'selected' fish. In test 1 ($\alpha = 49.5$, $\beta = 0.5$) we still expect a behavioural switch to occur at an order of every 100 days. However, we approximately double our prior's variance. In test 2 ($\alpha = 49$, $\beta = 1$) the expected rate of switching is halved.

To test the model's sensitivity to changes in the movement parameter priors, we varied the variances (δs) that describe the spread of each state and re-ran the adapted HMM for 10 randomly selected fish from each species. In test A, we increased all δ values by 10%, reflecting a prior expectation of greater variability between the parameters of individual fish, and in test B we decreased all δ values by 10%, reflecting an expectation of reduced variability. During all re-runs of the adapted HMM (Test A and Test B) the state transition prior is kept constant, therefore ensuring that any change in state is a direct consequence of the changes to the model's movement parameter prior.

2.5. Univariate modelling

To assess the advantages of using bivariate responses, we also carried out an analysis using a univariate observation model, considering only movements made in the horizontal dimension. The

same model for transition probabilities is used as described above. We apply this approach to the 34 fish (Atlantic cod, n=11; European plaice, n=23) previously characterized as data-rich movement paths. Reported comparisons reflect the percentage change, if any, in the resultant state sequences for each individual fish.

2.6. Inferring population patterns

Since population dynamics emerge as the sum of the individuals that comprise the population we used individual movement behaviours to explore spatiotemporal patterns. Annual temporal patterns of movement behaviour were calculated for each species in two ways. First, the daily individual probabilities of each fish being in each state were averaged across all individuals and over each week of the year. Secondly, the proportion of fish classified to each state was calculated by averaging the daily number of fish in each state and smoothing it, again to the weekly time step. Week refers to weeks of the year, starting on the 1st January and ending on the 31st December and is independent of year.

Patterns of space use while in either state were quantified using utilization distributions (Worton, 1989; Kie et al., 2010; Womble & Gende, 2013). For each species and sub-stock, utilization distributions were calculated by pooling all daily horizontal geolocations for specified time periods and spatially binning them into 5km² grid cells (Maxwell et al., 2011; Womble & Gende, 2013). Specified time periods were state dependent and based on a weekly averaged probability of observing a given state across all individuals exceeding 0.5. Successive weeks classified to the same behavioural state were then grouped. In Atlantic cod this meant locations that were classified

to a resident state between June – October and locations classified to a migrating state between November – May were used. In European plaice locations classified to a resident state between April – September and locations classified to a migrating state between October – March were used.

3. Results

3.1. Individual fish movement

Mapping the posterior probability of being in a particular state indicated that individual fish from either species switch between periods of highly directed movement when in a migratory state and periods of random and highly localized movements when in the less active resident state (Figure 3). Time spent in either state and the transitions between states were shown to vary in space and time and can be linked to certain habitats. For example, cod 1186 spent 197 days (June - November) consecutively in the resident state within the deeper waters of the Celtic Sea and only shifted into a migratory state when transiting through the English Channel. In comparison, plaice 1084 undertook long-distance directed movements after its release in the German Bight, spending 54 days consecutively in the migrating state before switching to the resident state in the shallow waters of the Central North Sea.

The majority of individual time series had observations that shifted between resident and migratory states (n=41 Atlantic cod, n=60 European plaice). However, a small number of individuals (n=6) persisted in a single state for the duration of their time series: one European plaice and four Atlantic

cod remained in a resident state throughout, whereas the movements of one Atlantic cod were consistently classified to the migratory state. All 6 single state movement paths had short duration times (average movement path duration = 56 ± 21 days) and were released throughout the year (November – May).

3.2. Population patterns

The mean probability of observing a resident state and the proportion of observations classified to a resident state varied throughout the year (Figure 4). In both species, migratory behaviour dominated throughout the winter and into spring, with the onset of summer signifying a shift in movement behaviour to the resident state. This shift in state occurred earlier in European plaice than in Atlantic cod, with movements of plaice having a higher probability of classification to the slower, less active resident state between late April and September, compared to June through to November in cod.

The model predicted large variation in average movement rates within each state (Table 1). Horizontal movement rates of plaice tagged and released in the Southern North Sea and German Bight were significantly lower than those tagged in the Central North Sea (resident, Student's *t*-test, $p < 0.001$; migrating, Student's *t*-test, $p < 0.001$). In the resident state, plaice from the Southern North Sea and German Bight moved on average 6.5 km day^{-1} horizontally and between $20.0\text{-}26.1 \text{ m day}^{-1}$ vertically compared to 13.9 km day^{-1} horizontally and between $15.6\text{-}125.8 \text{ m day}^{-1}$ vertically in the migratory state. In comparison, plaice tagged in the Central North Sea exhibited

much higher horizontal movement rates, moving on average 12.9 km day⁻¹ and 19.5 km day⁻¹ in the resident and migratory states, respectively.

Predicted spatial utilization distributions showed that migration occurred throughout the spatial domain, with no clear concentration of migratory activity in either species (Figure 5; Figure S8). In comparison, periods of time spent in a resident state produced clear geographical patches of space use while in certain habitats. These habitats varied with species (Figure 5) and sub-stock (Figure S8), however Southern North Sea cod and plaice both aggregated in the coastal waters off the English mainland. Cod in the English Channel shift to a resident state when in the western mouth of the Channel. In the German Bight, 90% of plaice spent most of their time at liberty within the area, displaying little or no dispersal. Of those plaice tagged in the Central North Sea, 48% were estimated to be in the resident state within the Northern North Sea whilst a further 11 fish undertook southern migrations before shifting to a resident mode in the shallow waters of the Central North Sea.

3.3. Prior sensitivity analysis

Minimal change in the classification of states was found during prior sensitivity analysis (Table S3). Re-running the HMM with changes to the transition probability prior revealed an average percentage change in state across all individuals of 1.5% in cod and 1.8% in plaice. In comparison, re-running the adapted HMM with changes to the movement parameters priors resulted in a percentage change in state that was on average <1% in cod and 2.3% in plaice. Such findings

demonstrate that the precise details of these priors are not crucial, with state classifications and biologically-important results being robust to fairly large changes in prior parameters.

3.4. Distribution of state dwell times

In an HMM, the length of time that an individual spends in one state before switching to the other necessarily follows a geometric distribution. Pooling across individuals, we find that these distributions are indeed geometric (see Figure S9 and Figure S10), and so the dynamics of the fitted changes in state are consistent with the Markov nature of the model. Further model assessment is provided by residual plots in Figure S11 and Figure S12.

3.5. Comparison to univariate modelling

State allocation was found to be different across the two tested observation models. The bivariate model resulted in state sequences that differed from the univariate model in 8.0% and 23.3% of cases in Atlantic cod and European plaice, respectively. This result confirms the need for the bivariate analysis.

4. Discussion

One of the main objectives of animal movement studies is the scaling of inference about movement behaviours from individuals to populations (Block et al., 2011; Wakefield et al., 2011; Raymond et al., 2015; Hays et al., 2016; Hindell et al., 2016). HMMs (Patterson et al., 2009; McKellar et al.,

2015; Michelot et al., 2016) or their Bayesian equivalents (Jonsen et al., 2013; McClintock et al., 2013) provide a powerful way of achieving this objective but only when movement behaviours are identified consistently across multiple individuals. Here we have achieved this consistency by ‘borrowing’ information from a finite sample of individuals and using it to provide our model with data-driven approximations of each state. Using this novel extension to HMM methodology, we investigated spatial and temporal shifts in movement behaviour from a large sample size of bivariate movement pathways. We demonstrated where and when shifts between two ecologically meaningful states are most likely to occur and add further confidence to observations of seasonal-dependence in the movements of commercially important demersal fish. Our biological findings complement and advance current understanding and highlight how our approach has significant utility in the fields of movement ecology and conservation.

Our approach to behaviour classification has two major advantages. First, it enabled us to gain meaningful inference from 73 (68% of the dataset) additional movement pathways, many of which are data-poor and would otherwise be subject to *post-hoc* removal. This retention of all individual-level information is favorable because it maximised our sample size and lends more information to our analysis. Second, our approach ensures that state labels are allocated consistently across multiple individuals, without resorting to large increases in model complexity. As a direct consequence of these two advantages, we were able to ask population-level *post-hoc* questions of our movement data and provide answers that are meaningful for conservation and spatial management.

Studies that classify behaviour based on horizontal and vertical movements are rare (but see Breed, Bowen, & Leonard, 2013; Bestley, Jonsen, Hindell, Harcourt, & Gales, 2015; DeRuiter et al., 2016). Here, we have assumed that h_t and v_t are conditionally dependent given latent states, which is a novel addition to the movement ecology literature. Our reasons for doing so are linked to *a priori* information about how the species of interest alter their activity levels within an annual cycle (e.g. Hobson et al., 2009). However, we intuitively expect other species occupying three-dimensional environments to exhibit similar degrees of coupling. For example, Bestley et al. (2015) reveal that the directed horizontal movements in multiple Antarctic pinniped species are associated with longer dive durations, whereas an inverted relationship is noted in blue whales (*Balaenoptera musculus*) with perceived shallow foraging behaviours being characterised by shallow dives and short horizontal movements (DeRuiter et al., 2016). Future studies may find similar observation models a powerful tool for investigating the dependences of horizontal and vertical movement rates (Carter, Bennett, Embling, Hosegood, & Russell, 2016).

Our estimates of average movement rates are consistent with previous work. In cod, horizontal movements rates whilst in the migratory state are shown to be approximately 13.5km day^{-1} which is comparable to past observations (Hobson et al., 2009) and laboratory studies (Bainbridge, 1957; Videler & Wardle, 1991). In plaice, previous research reports that seven tagged individuals swam on average $255 \pm 60.2\text{km}$ during pre-spawning migrations (Hunter, Metcalfe, & Reynolds, 2003). Assuming an average migrating of 2-4 weeks (as noted in Hunter et al., 2003), our estimates of horizontal movement rates between $13\text{-}20\text{km day}^{-1}$ seem reasonable. Therefore, we are confident that our choice of state labels is biologically meaningful for the species in question.

488 Much work has considered the horizontal and vertical movements of Atlantic cod (Hobson et al.,
489 2007, 2009) and European plaice (Hunter, Metcalfe, Arnold, et al., 2004; Hunter, Metcalfe,
490 O'Brien, et al., 2004), noting strong seasonal dependence in the movement patterns of individual
491 fish. Here we add confidence to these findings by providing a mechanistic view of how fish switch
492 between two movements modes during their annual cycle. Specifically, we show that cod and
493 plaice are more likely to occupy a resident state during the summer months (April – September in
494 plaice; June – November in cod). These periods are dominated by low horizontal and vertical
495 movement rates, therefore our findings support the hypothesis that both species spend their
496 summer in a sedentary state with minimal activity levels (Metcalfe et al., 2006; Righton et al.,
497 2010). Movement rates then ramp up during the winter and early spring (October – March in
498 plaice; December – May in cod), resulting in a collective shift in state. As in previous studies
499 (Hunter, Metcalfe, O'Brien, et al., 2004; Hobson et al., 2007), we interpret this shift to be reflective
500 of pre-spawning migrations, the onset of spawning and subsequent post-spawning migrations. One
501 limitation of the two-state model considered here is that we cannot directly infer foraging or
502 spawning behaviour. Foraging and spawning events are likely to represent an immediate activity
503 level, with both behaviours involving notable vertical displacement to and from the water column
504 (Hobson et al., 2009). The inclusion of a third immediate state would be a relatively
505 straightforward extension to model structure (see Vermard, Rivot, Mahévas, Marchal, & Gascuel,
506 2010; Peel & Good, 2011; Michelot et al., 2017 for examples of HMMs that consider >2 states).
507 However, it is unlikely that the scale of these vertical excursions is large enough to allow
508 classification at the daily time step. Therefore, we suggest that future studies either deploy more
509 sophisticated tags which are capable of recording more refined information about the underlying
510 movement process (e.g. accelerometers; Leos-Barajas, Photopoulou, et al., 2017) or consider a

nested hierarchical HMMs in which vertical and horizontal movements are recorded and classified at differing time scales (e.g. Leos-Barajas, Gangloff, et al., 2017).

Over the last 70 years, landings data for the North Sea and English Channel demonstrate that catch per unit effort (CPUE) for demersal species is higher during the summer months (Righton, Townhill, & Van Der Kooij, 2009). Such increases in CPUE are undoubtedly linked to changes in the populations' underlying movement behaviour, as time spent on the seabed results in an increased vulnerability to commercial exploitation (Righton et al., 2009). By assuming that time spent in a resident state is linked to sea-bottom dwelling, we show that cod and plaice aggregate in certain habitat types. For example, cod in the English Channel have greatest density in the deeper waters at the western mouth of the English Channel. In contrast, cod and plaice in the Southern North Sea aggregate in coastal waters off the English mainland. We also demonstrate that plaice in the German Bight remain exclusive within this region, suggesting the presence of a sedentary resident population in which fish spawn and forage in the same locality (previously noted in plaice by Hunter, Metcalfe, O'Brien, et al., 2004 and in cod by Neat et al., 2006). Such spatial information is essential for defining multi-species management measures, as strategies typically involve gear restrictions (Moustakas, Silvert, & Dimitromanolakis, 2006) aimed at limiting the exploitation of certain species/life stages and spatial fisheries closures aimed at protecting areas of particular importance for species survival e.g. foraging and spawning grounds (Hunter, Metcalfe, O'Brien, et al., 2004; Righton, Quayle, Hetherington, & Burt, 2007).

One limitation of our method is the way in which we deal with individual variation. Currently we assume that by analysing the movements of a finite sample of data-rich pathways (n=34) we gain

sufficient information about how the mean movement of each state is distributed throughout the population. We then expect the movements of all other individuals to be drawn from one of these distributions and make no attempt to explain any deviance away from this ‘expected’ process. One way to improve our approach and make it more generic would be the inclusion of covariate information (e.g. Phillips, Patterson, Leroy, Pilling, & Nicol, 2015). For example, 4 Atlantic cod were unexpectedly classified solely to a resident state even though their movements occurred throughout the winter (November – April). *Post-hoc* investigations reveal an average body length of ~56cm which lies within the predicted range of length at first maturity (31-74cm; Froese & Pauly, 2017). It is likely that immature fish act differently to their mature conspecifics (Sippel et al., 2015) and that tagging programmes like the one considered here include fish of differing sex and age (Carter et al., 2016). Consideration of these factors is beyond the scope of this paper. However we believe that the inclusion of body length (see Towner et al., 2016 for an ecological example) or other individual covariates within the HMMs likelihood function would provide a fruitful avenue for future research.

Technological advancements in telemetry devices have led to huge efforts to track the movements of free-roaming marine animals (Hussey et al., 2015; Hays et al., 2016). Tagging data is now seen as a valuable information source for stock assessment models (Sippel et al., 2015), monitoring the effectiveness of conservation efforts (e.g. Raymond et al., 2015; McGowan et al., 2017) and understanding population dynamics across vast spatial scales (e.g. Block et al., 2011; Hindell et al., 2016). However, there is no avoiding the fact that tags are expensive (McGowan et al., 2017), liable to occasional failure and often produce individual pathways that are of limited use (data-poor or a low number of observations). Here we have introduced a methodology that makes the

process of scaling up inference about movement behaviours from individuals to population more readily achievable. Moreover, we illustrate how the adoption of our approach can make tagging studies more cost-effective, as inference can still be gained from data-poor movement paths without resorting to redeployment or a renewed effort to secure further funding.

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Authors' contributions

C.A.G, T.A.P. and P.G.B. designed the methodology; C.A.G., P.G.B., J.L.B. and D.A.R. interpreted and analysed the model's output; movement paths were derived and analysed by D.A.R. and S.R.W.; C.A.G., J.L.B., P.G.B., D.A.R. and J.W.P. led the writing of the manuscript; C.A.G. and S.R.W. designed the figures. All authors contributed critically to the drafts and gave final approval for publication.

Data and R Code

The collated datasets for each fish species including estimated state sequences, geolocation estimates (latitude and longitude) and date stamps can be found on the CEFAS Data Hub (<https://doi.org/10.14466/CefasDataHub.54>). Example R code to run our HMM is included in Supplementary Information document 2 or can be downloaded from GitHub (https://github.com/cagriffiths1/Fish_HMM).

Conflict of Interest

Authors declare no conflicts of interest.

References

- Bainbridge, B. Y. R. (1957). The speed of swimming of fish as related to size and the frequency and amplitude of the tail beat. *The Journal of Experimental Biology*, 35(1937), 109–133. doi:10.1098/rspb.1971.0085
- Bestley, S., Jonsen, I. D., Hindell, M. A., Harcourt, R. G., & Gales, N. J. (2015). Taking animal tracking to new depths : synthesizing horizontal-vertical movement relationships for four marine predators. *Ecology*, 96(2), 417–427.
- Block, B. A., Jonsen, I. D., Jorgensen, S. J., Winship, A. J., Shaffer, S. A., Bograd, S. J., ... Costa, D. P. (2011). Tracking apex marine predator movements in a dynamic ocean. *Nature*, 475(7354), 86–90. doi:10.1038/nature10082
- Breed, G. A., Bowen, W. D., & Leonard, M. L. (2013). Behavioral signature of intraspecific competition and density dependence in colony-breeding marine predators. *Ecology and*

603 *Evolution*, 3(11), 3838–3854. doi:10.1002/ece3.754

604 Carter, M. I. D., Bennett, K. A., Embling, C. B., Hosegood, P. J., & Russell, D. J. F. (2016).
605 Navigating uncertain waters : a critical review of inferring foraging behaviour from location
606 and dive data in pinnipeds. *Movement Ecology*, 4–25. doi:10.1186/s40462-016-0090-9

607 Costa, D. P., Breed, G. A., & Robinson, P. W. (2012). New Insights into Pelagic Migrations:
608 Implications for Ecology and Conservation. *Annual Review of Ecology, Evolution, and*
609 *Systematics*, 43(1), 73–96. doi:10.1146/annurev-ecolsys-102710-145045

610 DeRuiter, S. L., Langrock, R., Skirbutas, T., Goldbogen, J. A., Chalambokidis, J., Friedlaender,
611 A. S., & Southall, B. L. (2016). A multivariate mixed hidden Markov model to analyze blue
612 whale diving behaviour during controlled sound exposures, *arXiv, arX*, 1–26.
613 doi:10.1214/16-AOAS1008

614 Froese, R., & Pauly, D. (2017). FishBase. World Wide Web electronic publication. Retrieved
615 from www.fishbase.org, version (10/2017)

616 GEBCO. (2017). General Bathymetric Chart of the Oceans. Retrieved 17 November 2016, from
617 http://www.bodc.ac.uk/projects/international/gebco/gebco_digital_atlas

618 Hays, G. C., Ferreira, L. C., Sequeira, A. M. M., Meekan, M. G., Duarte, C. M., Bailey, H., ...
619 Thums, M. (2016). Key Questions in Marine Megafauna Movement Ecology. *Trends in*
620 *Ecology and Evolution*, 31(6), 463–475. doi:10.1016/j.tree.2016.02.015

621 Hebblewhite, M., & Haydon, D. T. (2010). Distinguishing technology from biology: a critical
622 review of the use of GPS telemetry data in ecology. *Philosophical Transactions of the*
623 *Royal Society B: Biological Sciences*, 365(1550), 2303–2312. doi:10.1098/rstb.2010.0087

624 Hindell, M. A., McMahon, C. R., Bester, M. N., Boehme, L., Costa, D., Fedak, M. A., ...
625 Charrassin, J. B. (2016). Circumpolar habitat use in the southern elephant seal: Implications

for foraging success and population trajectories. *Ecosphere*, 7(5), 1–27.

doi:10.1002/ecs2.1213

Hobson, V. J., Righton, D., Metcalfe, J. D., & Hays, G. C. (2007). Vertical movements of North Sea cod. *Marine Ecology Progress Series*, 347, 101–110. doi:10.3354/meps07047

Hobson, V. J., Righton, D., Metcalfe, J. D., & Hays, G. C. (2009). Link between vertical and horizontal movement patterns of cod in the North Sea. *Aquatic Biology*, 5, 133–142.

doi:10.3354/ab00144

Hunter, E., Metcalfe, J. D., Arnold, G. P., & Reynolds, J. D. (2004). Impacts of migratory behaviour on population structure in North Sea plaice. *Journal of Animal Ecology*, 73, 377–385.

Hunter, E., Metcalfe, J. D., O'Brien, C. M., Arnold, G. P., & Reynolds, J. D. (2004). Vertical activity patterns of free-swimming adult plaice in the southern North Sea. *Marine Ecology Progress Series*, 279, 261–273. doi:10.3354/meps279261

Hunter, E., Metcalfe, J. D., & Reynolds, J. D. (2003). Migration route and spawning area fidelity by North Sea plaice. *Proceedings of the Royal Society B: Biological Sciences*, 270, 2097–2103. doi:10.1098/rspb.2003.

Hussey, N. E., Kessel, S. T., Aarestrup, K., Cooke, S. J., Cowley, P. D., Fisk, A. T., ... Whoriskey, F. G. (2015). Aquatic animal telemetry: A panoramic window into the underwater world. *Science*, 348(6240), 1255642. doi:10.1126/science.1255642

Jonsen, I. D. (2016). Joint estimation over multiple individuals improves behavioural state inference from animal movement data. *Scientific Reports*, 6, 20625. doi:10.1038/srep20625

Jonsen, I. D., Basson, M., Bestley, S., Bravington, M. V., Patterson, T. A., Pedersen, M. W., ...

Wotherspoon, S. J. (2013). State-space models for bio-loggers: A methodological road map.

649 *Deep Sea Research Part II*, 88–89, 34–46. doi:10.1016/j.dsr2.2012.07.008

650 Jonsen, I. D., Myers, R. A., & James, M. C. (2007). Identifying leatherback turtle foraging
651 behaviour from satellite telemetry using a switching state-space model. *Marine Ecology*
652 *Progress Series*, 337, 255–264.

653 Kahle, D., & Wickham, H. (2013). ggmap: Spatial Visualization with ggplot2. *The R Journal*, 5,
654 144–161.

655 Kie, J. G., Matthiopoulos, J., Fieberg, J., Powell, R. A., Cagnacci, F., Mitchell, M. S., ...
656 Moorcroft, P. R. (2010). The home-range concept: are traditional estimators still relevant
657 with modern telemetry technology? *Philosophical Transactions of the Royal Society B:*
658 *Biological Sciences*, 365, 2221–2231. doi:10.1098/rstb.2010.0093

659 Kranstauber, B., Cameron, A., Weinzerl, R., Fountain, T., Tilak, S., Wikelski, M., & Kays, R.
660 (2011). The Movebank data model for animal tracking. *Environmental Modelling and*
661 *Software*, 26, 834–835. doi:10.1016/j.envsoft.2010.12.005

662 Langrock, R., King, R., Matthiopoulos, J., Thomas, L., Fortin, D., & Morales, J. M. (2012).
663 Flexible and practical modeling of animal telemetry data : hidden Markov models and
664 extensions. *Ecology*, 93(11), 2336–2342.

665 Leos-Barajas, V., Gangloff, E. J., Adam, T., Langrock, R., van Beest, F. M., Nabe-Nielsen, J., &
666 Morales, J. M. (2017). Multi-scale Modeling of Animal Movement and General Behavior
667 Data Using Hidden Markov Models with Hierarchical Structures. *Journal of Agricultural,*
668 *Biological, and Environmental Statistics*, 22(3), 232–248. doi:10.1007/s13253-017-0282-9

669 Leos-Barajas, V., Photopoulou, T., Langrock, R., Patterson, T. A., Watanabe, Y., Murgatroyd,
670 M., & Papastamatiou, Y. P. (2017). Analysis of animal accelerometer data using hidden
671 Markov models. *Methods in Ecology and Evolution*, 8(2), 161–173. doi:10.1111/2041-

672 210X.12657

673 Lindberg, M. S., & Walker, J. (2007). Satellite Telemetry in Avian Research and Management:
674 Sample Size Considerations. *Journal of Wildlife Management*, 71(3), 1002–1009.
675 doi:10.2193/2005-696

676 Maxwell, S. M., Breed, G. A., Nickel, B. A., Makanga-Bahouna, J., Pemo-Makaya, E., Parnell,
677 R. J., ... Coyne, M. S. (2011). Using satellite tracking to optimize protection of long-lived
678 marine species: Olive ridley sea turtle conservation in central africa. *PLoS ONE*, 6(5),
679 e19905. doi:10.1371/journal.pone.0019905

680 McClintock, B. T., Russell, D. J. F., Matthiopoulos, J., & King, R. (2013). Combining individual
681 animal movement and ancillary biotelemetry data to investigate population-level activity
682 budgets. *Ecology*, 94(4), 838–849. doi:10.1890/12-0954.1

683 McGowan, J., Beger, M., Lewison, R. L., Harcourt, R., Campbell, H., Priest, M., ... Possingham,
684 H. P. (2017). Integrating research using animal-borne telemetry with the needs of
685 conservation management. *Journal of Applied Ecology*, 54(2), 423–429. doi:10.1111/1365-
686 2664.12755

687 McKellar, A. E., Langrock, R., Walters, J. R., & Kesler, D. C. (2015). Using mixed hidden
688 Markov models to examine behavioral states in a cooperatively breeding bird. *Behavioral*
689 *Ecology*, 26(1), 148–157. doi:10.1093/beheco/aru171

690 Metcalfe, J. D., & Arnold, G. (1997). Tracking fish with electronic tags. *Nature*, 387, 665–666.
691 doi:10.1038/42622

692 Metcalfe, J. D., Hunter, E., & Buckley, A. A. (2006). The migratory behaviour of North Sea
693 plaice: Currents, clocks and clues. *Marine and Freshwater Behaviour and Physiology*,
694 39(1), 25–36. doi:10.1080/10236240600563404

695 Michelot, T., Langrock, R., Bestley, S., Jonsen, I. D., Photopoulou, T., & Patterson, T. A.
 696 (2017). Estimation and simulation of foraging trips in land-based marine predators.
 697 *Ecology*, 98(7), 1932–1944. doi:10.1002/ecy.1880
 698 Michelot, T., Langrock, R., & Patterson, T. (2016). moveHMM: An R package for the statistical
 699 modelling of animal movement data using hidden Markov models. *Methods in Ecology and*
 700 *Evolution*, 7, 1308–1315. doi:10.1111/2041-210X.12578
 701 Moustakas, A., Silvert, W., & Dimitromanolakis, A. (2006). A spatially explicit learning model
 702 of migratory fish and fishers for evaluating closed areas. *Ecological Modelling*, 192, 245–
 703 258. doi:10.1016/j.ecolmodel.2005.07.007
 704 Neat, F. C., Bendall, V., Berx, B., Wright, P. J., Cuaig, M., Townhill, B., ... Righton, D. (2014).
 705 Movement of Atlantic cod around the British Isles: Implications for finer scale stock
 706 management. *Journal of Applied Ecology*, 51, 1564–1574. doi:10.1111/1365-2664.12343
 707 Neat, F. C., Wright, P. J., Zuur, A. F., Gibb, I. M., Gibb, F. M., Tulett, D., ... Turner, R. J.
 708 (2006). Residency and depth movements of a coastal group of Atlantic cod (*Gadus morhua*
 709 L.). *Marine Biology*, 148, 643–654. doi:10.1007/s00227-005-0110-6
 710 Nguyen, V. M., Brooks, J. L., Young, N., Lennox, R. J., Haddaway, N., Whoriskey, F. G., ...
 711 Cooke, S. J. (2017). To share or not to share in the emerging era of big data: perspectives
 712 from fish telemetry researchers on data sharing. *Canadian Journal of Fisheries and Aquatic*
 713 *Sciences*, 74, 1260–1274. doi:10.1139/cjfas-2016-0261
 714 Ogburn, M. B., Harrison, A.-L., Whoriskey, F. G., Cooke, S. J., Mills Flemming, J. E., & Torres,
 715 L. G. (2017). Addressing Challenges in the Application of Animal Movement Ecology to
 716 Aquatic Conservation and Management. *Frontiers in Marine Science*, 4, 70.
 717 doi:10.3389/fmars.2017.00070

718 Patterson, T. A., Basson, M., Bravington, M. V., & Gunn, J. S. (2009). Classifying movement
 719 behaviour in relation to environmental conditions using hidden Markov models. *Journal of*
 720 *Animal Ecology*, 78(6), 1113–1123. doi:10.1111/j.1365-2656.2009.01583.x
 721 Patterson, T. A., Parton, A., Langrock, R., Blackwell, P. G., Thomas, L., & King, R. (2017).
 722 Statistical modelling of individual animal movement: an overview of key methods and a
 723 discussion of practical challenges. *AStA Advances in Statistical Analysis*, 101, 399–438.
 724 doi:10.1007/s10182-017-0302-7
 725 Pedersen, M. W., Righton, D., Thygesen, U. H., Andersen, K. H., & Madsen, H. (2008).
 726 Geolocation of North Sea cod (*Gadus morhua*) using hidden Markov models and
 727 behavioural switching. *Canadian Journal of Fisheries and Aquatic Sciences*, 65, 2367–
 728 2377. doi:10.1139/F08-144
 729 Peel, D., & Good, N. M. (2011). A hidden Markov model approach for determining vessel
 730 activity from vessel monitoring system data. *Canadian Journal of Fisheries and Aquatic*
 731 *Sciences*, 68, 1252–1264. doi:10.1139/f2011-055
 732 Phillips, J. S., Patterson, T. A., Leroy, B., Pilling, G. M., & Nicol, S. J. (2015). Objective
 733 classification of latent behavioral states in bio-logging data using multivariate-normal
 734 hidden Markov models. *Ecological Applications*, 25(5), 1244–1258. doi:10.1890/14-
 735 0862.1.sm
 736 Pittman, S. J., Monaco, M. E., Friedlander, A. M., Legare, B., Nemeth, R. S., Kendall, M. S., ...
 737 Caldwell, C. (2014). Fish with chips: Tracking reef fish movements to evaluate size and
 738 connectivity of Caribbean marine protected areas. *PLoS ONE*, 9(5), e96028.
 739 doi:10.1371/journal.pone.0096028
 740 R Development Core Team. (2016). A Language and Environment for Statistical Computing. R

741 Foundation for Statistical Computing, Vienna.

742 Raymond, B., Lea, M. A., Patterson, T., Andrews-Goff, V., Sharples, R., Charrassin, J. B., ...

743 Hindell, M. A. (2015). Important marine habitat off east Antarctica revealed by two decades

744 of multi-species predator tracking. *Ecography*, 38, 121–129. doi:10.1111/ecog.01021

745 Righton, D. A., Andersen, K. H., Neat, F., Thorsteinsson, V., Steingrund, P., Svedäng, H., ...

746 Metcalfe, J. D. (2010). Thermal niche of Atlantic cod *Gadus morhua*: Limits, tolerance and

747 optima. *Marine Ecology Progress Series*, 420, 1–13. doi:10.3354/meps08889

748 Righton, D. A., Metcalfe, J. D., & Connolly, P. (2001). Different behaviour of North and Irish

749 Sea cod. *Nature*, 411(90), 2001.

750 Righton, D. A., Quayle, V. A., Hetherington, S., & Burt, G. (2007). Movements and distribution

751 of cod (*Gadus morhua*) in the southern North Sea and English Channel: Results from

752 conventional and electronic tagging experiments. *Journal of the Marine Biological*

753 *Association of the United Kingdom*, 87, 599–613. doi:10.1017/S0025315407054641

754 Righton, D. A., Townhill, B., & Van Der Kooij, J. (2009). Catch me if you can: archival tagging

755 studies can help assess changes in the accessibility of Atlantic cod (*Gadus morhua*) to trawl

756 gears. ICES CM 2009/J:08. *ICES CM*, J:08.

757 Scott, R., Hodgson, D. J., Witt, M. J., Coyne, M. S., Adnyana, W., Blumenthal, J. M., ... Godley,

758 B. J. (2012). Global analysis of satellite tracking data shows that adult green turtles are

759 significantly aggregated in Marine Protected Areas. *Global Ecology and Biogeography*, 21,

760 1053–1061. doi:10.1111/j.1466-8238.2011.00757.x

761 Sippel, T., Paige Eveson, J., Galuardi, B., Lam, C., Hoyle, S., Maunder, M., ... Nicol, S. (2015).

762 Using movement data from electronic tags in fisheries stock assessment: A review of

763 models, technology and experimental design. *Fisheries Research*, 163, 152–160.

doi:10.1016/j.fishres.2014.04.006

Towner, A. V., Leos-Barajas, V., Langrock, R., Schick, R. S., Smale, M. J., Kaschke, T., ...

Hopkins, W. (2016). Sex-specific and individual preferences for hunting strategies in white sharks. *Functional Ecology*, 30(8), 1397–1407. doi:10.1111/1365-2435.12613

Vermard, Y., Rivot, E., Mahévas, S., Marchal, P., & Gascuel, D. (2010). Identifying fishing trip behaviour and estimating fishing effort from VMS data using Bayesian Hidden Markov Models. *Ecological Modelling*, 221, 1757–1769. doi:10.1016/j.ecolmodel.2010.04.005

Videler, J. J., & Wardle, C. S. (1991). Fish swimming stride by stride: speed limits and endurance. *Reviews in Fish Biology and Fisheries*, 1, 23–40. doi:10.1007/BF00042660

Wakefield, E. D., Phillips, R. A., Trathan, P. N., Arata, J., Gales, R., Huin, N., ... Matthiopoulos, J. (2011). Habitat preference , accessibility , and competition limit the global distribution of breeding Black-browed Albatrosses. *Ecological Monographs*, 81(1), 141–167.

Wickham, H. (2009). ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York.

Womble, J. N., & Gende, S. M. (2013). Post-Breeding Season Migrations of a Top Predator, the Harbor Seal (*Phoca vitulina richardii*), from a Marine Protected Area in Alaska. *PLoS ONE*, 8(2), e55386. doi:10.1371/journal.pone.0055386

Worton, B. J. (1989). Kernel Methods for Estimating the Utilization Distribution in Home-Range Studies. *Ecology*, 70(1), 164–168.

Zucchini, W., MacDonald, I. L., & Langrock, R. (2016). *Hidden Markov models for time series: an introduction using R (second edition)*. Chapman and Hall/CRC.

Tables

Table 1. State dependent movement rates (horizontal: km day⁻¹, vertical: m day⁻¹) by sub-stock in Atlantic cod and European plaice. All values are taken from collated model output and are averaged across all individuals.

	<i>Sub-Stock</i>	Resident state		Migrating state	
		<i>Horizontal movement (km)</i>	<i>Vertical movement (m)</i>	<i>Horizontal movement (km)</i>	<i>Vertical movement (m)</i>
Atlantic cod (<i>Gadus morhua</i>)	Southern North Sea	9.2	31.5	13.9	158.3
	English Channel	9.6	53.5	13.4	125.4
European plaice (<i>Pleuronectes platessa</i>)	Southern North Sea	6.4	20.0	12.9	115.6
	German Bight	6.6	26.1	14.9	125.8
	Central North Sea	12.9	26.2	19.5	121.0

Figure Legends

Figure 1. Release locations of all tagged fish. Atlantic cod, *Gadus morhua* (n=46) are shown in red, fish are either separated into the English Channel sub-stock (triangles, n=23) or the Southern North Sea sub-stock (circles, n=23). European plaice, *Pleuronectes platessa* (n=61) are shown in purple, fish are grouped into three sub-stocks: Central North Sea (circles, n=27), German Bight (triangles, n=10) or Southern North Sea (crosses, n=24).

Figure 2. Estimated state-dependent distributions (bars) for vertical (left) and horizontal (right) movements of all 34-selected fish. Black lines illustrate the movement parameter prior distributions $N(m, \delta)$ that were constructed based on collective model output. Prior distributions are state (resident, solid line; migratory, dashed line), species (Atlantic cod, top; European plaice, bottom) and dimension (horizontal or vertical) specific.

Figure 3. State dependent movement behaviour of two individual fish. Shown in a color scale from red to yellow is the movement behaviour of one Atlantic cod tagged on the 25th March 2005 (duration = 300 days). Red points represent a migrating state, yellow a resident state and those points shown in orange illustrate times when the model was uncertain of state classification (i.e. the daily probability of state classification was less than 0.85). Shown in a scale from purple to cyan is the movement behaviour of one European plaice tagged on the 14th November 1997 (duration = 253 days). Purple points represent a migrating state, cyan a resident state and those points shown in royal blue illustrate times when the model was uncertain of state classification. The start and end point of each individual's movement path are shown as a green triangle and a red diamond, respectively.

Figure 4. Annual temporal distributions of the resident state in Atlantic cod (red) and European plaice (blue). The plotted line in either graph illustrates the mean probability of observing a resident state (± 1 SE – grey shading). The underlying barplots demonstrate the proportion of individual fish that are in a resident state during each week. Periods of time when the mean probability of observing a resident state is continually >0.5 are illustrated in either species.

Figure 5. Annual state dependent space use patterns of Atlantic cod (A and B) and European plaice (C and D) in the North Sea and English Channel. Plots are split into periods of resident dominant (A and C) and migrating dominant (B and D), defined by a mean probability of observing a given state at a given time being > 0.5 . All grid cells (5km^2) are illustrated in a color gradient so as to illustrate the sum total number of days spent in a certain state in a given grid cell within a specified time period.

Figure 1.

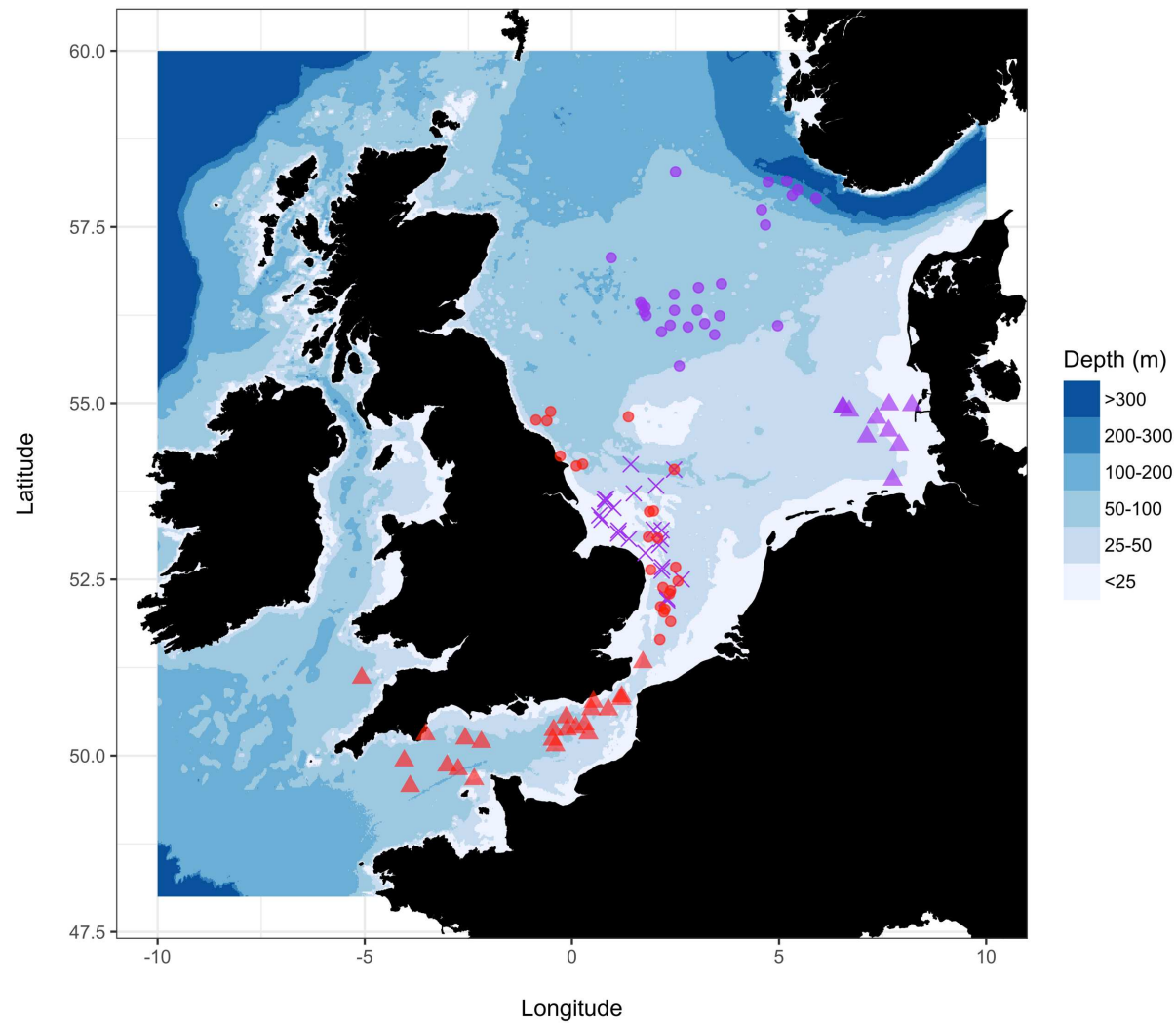
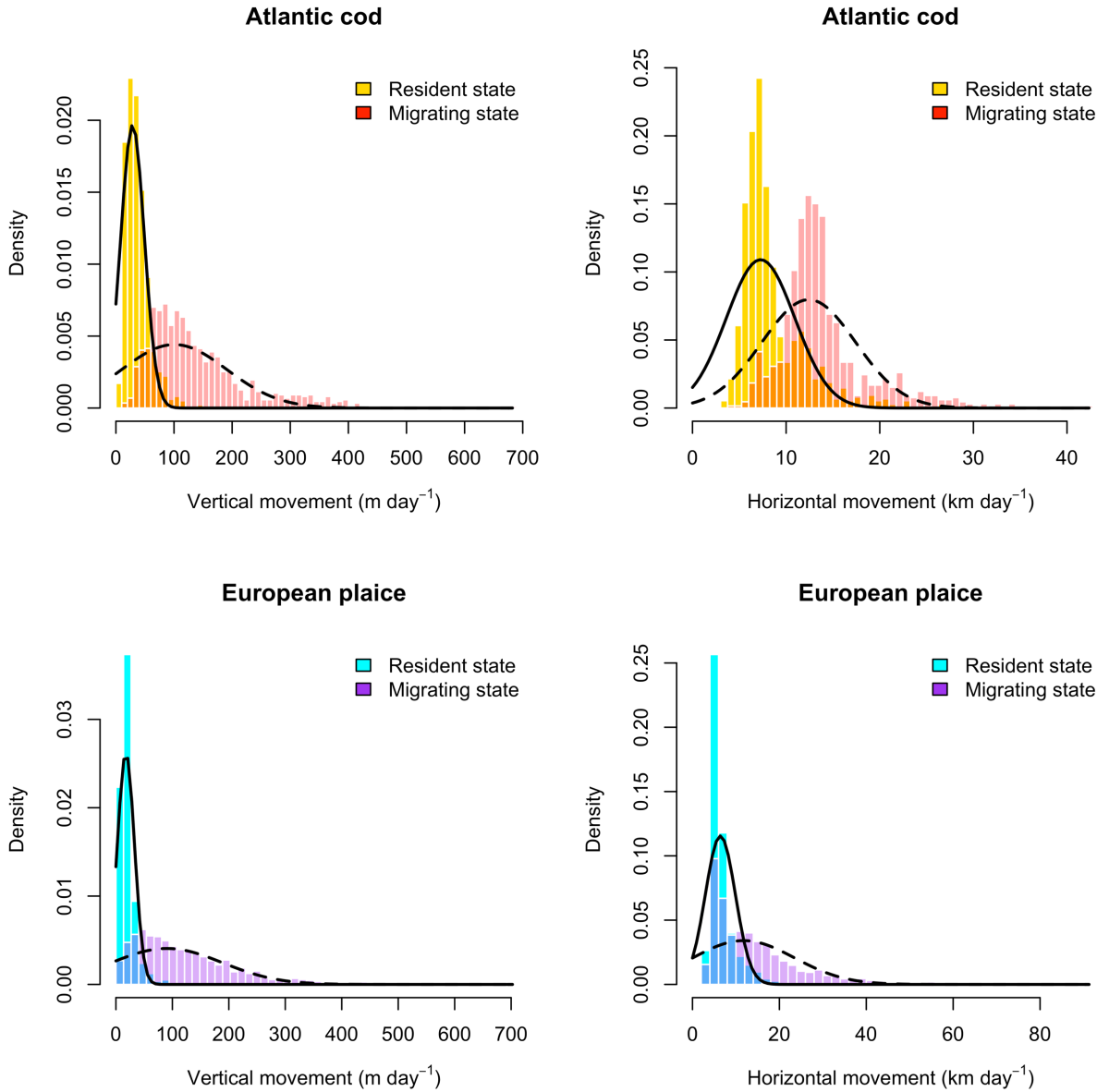
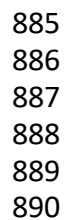


Figure 2.



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891 **Figure 4.**
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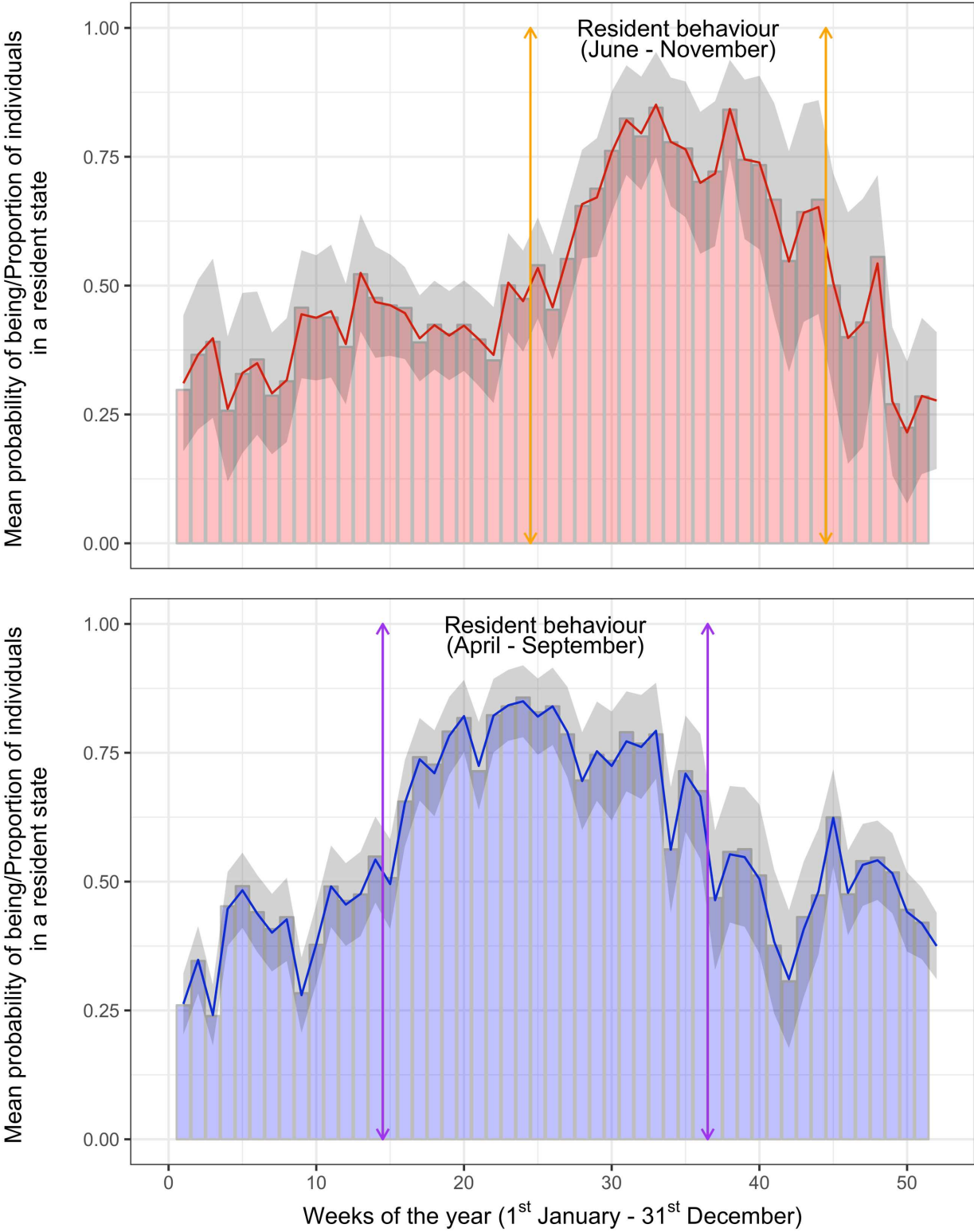


Figure 5.

